

INHERITANCE OF SEED SHAPE, HERITABILITIES
AND CORRELATIONS AMONG RELATED TRAITS
IN PEANUT (Arachis hypogaea L.)

BY

PICKFORD K. SIBALE

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1984

ACKNOWLEDGEMENTS

The author wishes to express his sincere appreciation to Dr. A. J. Norden for his guidance, assistance and encouragement during the course of these studies; and to Drs. D. W. Gorbet, E. S. Horner, W. G. Blue and P. M. Lyrene for serving on the supervisory committee and critically reviewing the manuscript.

Sincere appreciation is extended to the Malawi Government for granting him a 36-month study leave and to USAID for financial support.

Special thanks are due to Mr. A. Chiremba for assistance in the development of computer programs for statistical analyses and to Dr. C. J. Wilcox for statistical advice.

Thanks are also given to Maria I. Cruz for typing this manuscript.

The author wishes to express much appreciation to his wife Elizabeth for her understanding and encouragement.

TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.	ii
LIST OF TABLES.	iv
LIST OF FIGURES	vi
ABSTRACT.	vii
INTRODUCTION.	1
LITERATURE REVIEW	3
Seed Shape as Related to Blanchability in Peanut . . .	4
Inheritance Studies	5
Correlation and Heritability Studies.	7
MATERIALS AND METHODS	9
RESULTS AND DISCUSSIONS	20
Parental Generations.	20
Hybrid Generations.	20
Means and Ranges for Pod Length, Pod Breadth, Pod Constriction and Seed Shape.	21
Inheritance of Seed Shape	33
Proposed Genetic Model	41
Heritabilities and Correlations	43
Relative Efficiency of Indirect Selection of Trait (x) due to Selection for Trait (y)	47
Breeding Implications	49
SUMMARY AND CONCLUSIONS	51
LITERATURE CITED.	53
BIOGRAPHICAL SKETCH	57

LIST OF TABLES

Table		Page
1	Varieties and experimental lines used as parents in crosses to determine the inheritance of seed shape in peanut.	9
2	Seed shapes of six peanut genotypes involved in the crosses.	10
3	Relevant parts of the analysis of variance and mean square expectations	18
4	Means and ranges for Pod Length, Pod Breath, Pod Constriction and seed shape for parents and F_1 pods bearing F_2 seeds	21
5	Means and ranges for Pod Length, Pod Breath, Pod Constriction and seed shape for parents and F_2 pods bearing F_3 seeds	24
6	Means and ranges for Pod Length, Pod Breath, Pod Constriction and seed shape for parents and the F_3 pods bearing F_4 seeds	27
7	F_2 seed segregation data in Crosses 628, 629, 630, 632 and 634 analyzed by chi-square test for goodness-of-fit to the ratio 3:1	34
8	F_2 seed segregation data in Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.	35
9	F_3 seed segregation data in Crosses 628, 629, 630 and 632 analyzed by chi-square test for goodness-of-fit to the ratio 5:3.	37
10	F_3 seed segregation data for Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.	38
11	F_4 seed segregation data in Crosses 628, 629, 630 and 632 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.	39
12	F_4 seed segregation data in Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.	40

Table		Page
13	Proposed gene symbols for the seed shape of the parents used in crosses to investigate the mode of inheritance of seed shape.	42
14	Phenotypic (r_p) and genotypic (r_g) correlation estimates among traits and their heritabilities (h^2).	44
15	Relative efficiency of indirect selection of trait (x) due to selection for trait (y).	48

LIST OF FIGURES

Figure		Page
1	Profile of pod dimensions measured.	13
2	An example of contrasting seed shapes in two peanut genotypes used in the study.	14

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

INHERITANCE OF SEED SHAPE, HERITABILITIES
AND CORRELATIONS AMONG RELATED TRAITS
IN PEANUTS (Arachis hypogaea L.)

By

Pickford K. Sibale

April 1984

Chairman: A. J. Norden
Major Department: Agronomy

A study was conducted to determine the mode of inheritance of seed shape in peanut (Arachis hypogaea L.). Estimates of heritability for pod length, pod breadth, pod constriction index, pod shape index and seed shape were obtained. Seed shape classifications were based on the presence or absence of the flat surface at the ends where the two seeds meet inside a two-loculed pod. The genotypic and phenotypic correlations among the five traits were also determined. The study involved five crosses and their reciprocals, and the progenies up to the F_4 seed generation were analyzed.

The results indicate that in four of the five crosses, the inheritance of seed shape was monogenically controlled with the flat-end shape (SS) being dominant over the smooth-end shape (ss). In one cross, the inheritance of seed shape could not be determined, probably due to the presence of other factors.

Heritability estimates for the five traits were low, ranging from 0.54 for pod length to 0.26 for seed shape. This suggests that

selection for improved (smooth-end) seed shape would be more effective in later (F_5 - F_6) generations.

Genotypic correlations among traits were generally higher than phenotypic correlations. The analysis of data to determine the relative efficiencies of indirect selection of related traits for the improvement of seed shape showed that seed shape improvement can best be achieved by directly selecting for seed shape itself or by indirectly selecting for increased pod shape index. The next best alternative is through the indirect selection for longer pods.

INTRODUCTION

Seed shape is an important consideration in the peanut (Arachis hypogaea L.) processing industry because it determines the quality and consumer acceptance of peanut products. It is known to affect the blanchability of roasted peanuts, for instance, thereby indirectly affecting the market value of the finished product.

There are a number of different shapes of seeds observed both within and between peanut cultivars, and such differences have variously been attributed to both physiological and genetic causal factors. The terminology used to describe the various shapes of seeds also varies considerably depending on the objectives of the researcher and the precision with which the seed shape is quantified.

In this investigation the notation "flat seed" refers only to the flat surface, common to both the apical and basal seeds originating from the same pod, where they touch each other. The absence of the "flat seed" shape has been referred to as "round, smooth" shape which is indicative of lack of contact between the basal and apical seeds inside the pod.

Knowledge of the mode of inheritance of peanut seed shape and of the relationship between pod traits and seed shape would be useful in assisting the breeder to select superior individuals from a segregating population.

Previous studies on the mode of inheritance of peanut seed shape have not provided consistent information since, in most cases, the studies were made on limited breeding populations where seed shape was but one of the features being studied. It has also been suggested that differences in reported modes of inheritance could have been due to possible physiological maternal influence rather than the genotype itself in the expression of peanut seed shape.

The objective of this research was to establish the mode of inheritance of peanut seed shape on large populations derived from crosses among genotypes with contrasting seed shapes.

LITERATURE REVIEW

Studies on the inheritance of seed shape in crop plants began with Mendel's (1865) experiment on round versus wrinkled seed shape in the common pea (Pisum sativum L.). When Mendel crossed plants from the true breeding strain having round seeds with plants from the true breeding strain having wrinkled seeds, he observed in the F_2 generation an almost perfect ratio of 3 round:1 wrinkled seeds. Mendel accounted for the 3:1 ratio in the F_2 by reasoning that the phenotype "round seeds" was dominant and "wrinkled seeds" was recessive. He assumed that when the F_1 hybrids form gametes, half the gametes carry the dominant "A" allele and half carry the recessive "a" allele. Combining gametes at random from two such plants yields a genetic ratio in the F_2 of $1/4AA:1/2Aa:1/4aa$, but since "A" is the dominant allele, the observed ratio of phenotype in the F_2 is 3 round:1 wrinkled.

This scheme of inheritance, which Mendel was the first to enunciate, has since been confirmed in peas and other crop plants and has also been found to hold good for such diverse traits as height, hairiness, flower color, shape of pollen grains, the structure of fruits, etc. (Punnett, 1911).

However, deviations in phenotype from Mendelian segregation have been reported. Working on the same traits in peas as Mendel, Pchelarov (1972) reported that when green wrinkled-seeded varieties

were crossed with varieties having yellow round seeds, a larger number of the later type segregated in the F_2 than was expected on the basis of Mendelian laws. It has shown that changes in the shape (round) and color (yellow) of the seeds can arise as a result of the effect of sunlight and high temperatures. When grown in normal conditions they give plants with green wrinkled seeds. The temperature effect on the expression of a trait was later shown to operate in altering the expression of certain traits in *Drosophila* (Plunkett 1926, Gardner and Woolf 1950). However, such reports on deviations from Mendelian segregation are rare in the literature.

Seed Shape as Related to Blanchability in Peanut

Blanchability of kernels is an important consideration in the peanut processing industry and peanuts that blanch readily are highly desirable (Farouk et al., 1977). Even though there appears to be no standard blanching procedure in the peanut processing industry (Tiemstra, 1973), some causal factors related to the blanchability of peanut kernels have been identified. Some of these factors are related to the physical properties of the kernels whereas others are due to the physical stresses imposed on the peanut kernels during the blanching process.

Of the latter causal factors, Shackelford (1972) identified temperature and amount of moisture removed as factors affecting blanchability of peanuts. This confirmed earlier work by Beasley and Dickens (1963) who had shown that the amount and rate of moisture removal affected blanchability more than did temperature.

Woodward (1973) found that the tensile strength of the peanut skin decreased with increased drying rate. The increased skin stress condition at high drying rates leads to skin rupture or differential dimensional response between kernel and skin thereby enhancing blanchability.

Farouk et al. (1977) indicated that skin moisture content and repeated rewetting and drying cycles improved blanchability of spanish-peanut kernels under constant drying air temperature and relative humidity.

Among the physical properties of the kernels that affect blanchability, Tiemstra (1973) reported that shrivels and maturity of kernels are two important factors affecting blanchability.

In addition, seed shape is also known to affect the blanchability of peanuts (Norden et al., 1982; Metelerkamp and Hilderbrand 1975) especially where mechanical methods of blanching are used. Peanut varieties that have a large percentage of flat ended seeds are difficult to blanch mechanically (Coffelt and Hammons 1974a) and also show a greater tendency to split during mechanical shelling.

Inheritance Studies

The shape of peanut seeds is determined, to a large extent, by the shape of the pod. The pod characteristics could even mask the genetic expression of seed characteristics (Godoy and Norden 1981), particularly in segregating populations.

It is the presence or absence of pod constriction which determines whether or not seeds have flattened ends that are in contact with the other seed in the pod. Pods without constriction tend to have seeds with flattened ends.

Studies on the mode of inheritance of pod constriction have produced contradictory results. Badami (in Hunter and Leake, 1933) was the first to propose that the absence of pod constriction was dominant to its presence. He described four groups on the basis of the depth of constriction and concluded that two factors were involved, with the cylindrical type being the double dominant.

Hassan (1964) confirmed Badami's proposal but, instead, proposed a trigenic complementary model with an F_2 phenotypic ratio of 45:19. He assumed that A is a basic gene with B and C complementary to A, but not to each other. Accordingly, shallow constriction appears when A is present together with B or C or both.

However, Mauboussin (unpublished data), as cited by Hammons (1973), proposed that the presence of pod constriction is dominant to the absence of pod constriction.

Coffelt and Hammons (1974a) confirmed Mauboussin's proposal. Their results indicate that the two peanut cultivars, Argentine and Early Runner, differ at three unlinked nuclear loci and for one cytoplasmic factor conditioning pod constriction. These four factors interact in a complementary-duplicate manner. Three dominant alleles, one at each of any three of the four factors, are required for the presence of pod constriction. Any two homozygous recessive factors result in unconstricted pods. They proposed gene symbols Pc_1 , Pc_2

and Pc_3 for the nuclear genes and the symbol A for the cytoplasmic factors.

Relatively few studies have been reported in the literature regarding the mode of inheritance of seed shape in peanuts.

Hayes (1933) was the first to propose a model of gene action for peanut seed shape. In a limited population of segregating material from a cross involving Valentine (long-seeded) and Sine (short-seeded) varieties, he concluded that long seed was dominant over short seed in a ratio of 15:1, thus suggesting the presence of two factors governing the seed shape trait.

From F_2 and F_3 plants of crosses between long-seeded (runner) and short-seeded (spanish) types, Hull (1937) obtained a clear-cut 1 long:2 intermediate:1 short ratio, with no detectable dominance. He also observed considerable variation in the shape of seeds from any one plant and he suggested a possible physiological maternal influence rather than the genotype itself in the expression of seed shape.

Studies on the mode of inheritance in crosses involving the Gujarat narrow leaf mutant led Balaiah et al. (1977) to conclude that kernel shape was inherited in a simple Mendelian ratio of 3 oblong:1 round.

Correlation and Heritability Studies

Correlation and heritability estimates are useful in breeding programs because they reveal the interdependence between traits, and they also show how heritable the traits are; thus, they assist in the process of selecting superior individuals from a population.

Many quantitative traits pertaining to yield, plant vigor and seed quality in peanuts have been studied (Hammons, 1973). However, the relationships between various pod traits (i.e., pod length, pod breadth, pod length/pod breadth ratio, pod constriction and seed shape) have rarely been reported in the literature. On the other hand, heritability estimates for most pod traits have been reported.

Coffelt and Hammons (1974b) found high heritability estimates for pod length, pod breadth and pod length/pod breadth ratio, which was in agreement with heritability estimates obtained by Majumdar et al. (1969). This indicates that parental lines superior in these pod traits can be used in crosses with a reasonable expectation of obtaining the parental type in the progeny. Mohammed et al. (1978) also reported high estimates of heritability for pod length with values ranging from 0.79 to 0.92.

MATERIALS AND METHODS

Six peanut genotypes were selected for this study and were utilized in five different crosses and their reciprocals, with Chalimbana peanut variety as the common parent. Table 1 shows the identification numbers of the crosses and their reciprocals.

Table 1. Varieties and experimental lines used as parents in crosses to determine the inheritance of seed shape in peanut.

Cross number	Parentage	
628A	Chalimbana	x UF 78114
628B (Reciprocal)	UF 78114	x Chalimbana
629A	Chalimbana	x Early Bunch
629B (Reciprocal)	Early Bunch	x Chalimbana
630A	Chalimbana	x Florunner
630B (Reciprocal)	Florunner	x Chalimbana
632A	Chalimbana	x Florigiant
632B (Reciprocal)	Florigiant	x Chalimbana
634A	Chalimbana	x UF 714021
634B (Reciprocal)	UF 714021	x Chalimbana

The six genotypes were selected on the basis of similarities or differences in seed shape as compared with Chalimbana, the common parent in all the crosses. Table 2 shows the type of seed shape for each of the six genotypes used.

Table 2. Seed shapes of six peanut genotypes involved in the crosses.

Variety	Type of seed shape*
Chalimbana	Flat end surface
UF 78114	Smooth rounded end surface
Early Bunch	Smooth rounded end surface
Florunner	Flat end surface
Florigiant	Smooth rounded end surface
UF 714021	Smooth rounded end surface

* A 10 pod sample was used to characterize the seed shape for each variety.

The other characteristics related to each genotype can be described as follows:

Chalimbana is an alternately branched runner with relatively unstricted pods of the Jumbo runner pod group (Gibbons and Tattersfield, 1969; Brown, 1965). Chalimbana generally has two-loculed pods, with a few single and three-loculed pods. Kernel color is dark tan and has a 100 kernel weight of approximately 100 grams. The kernels are difficult to blanch because of the flat seed shape. It matures about 145 days from planting.

Florunner is derived from a cross between Early Runner and Florispan. The pods and seeds of Florunner are slightly larger, thicker and lighter in color than pods and seeds of Early Runner (Norden et al., 1969). It has relatively constricted pods thereby producing seeds that have flat ends. It matures in approximately 135 days.

Early Bunch has a spreading bunch growth habit. Seeds are of the Virginia market type weighing about 105 g per 100 seeds. The cultivar is characterized as having uniform, well-filled pods. It has oblong seed slightly darker pink than seeds of Florigiant (Norden et al., 1977).

Florigiant has a spreading growth habit. Pods are generally large, uniform, and cylindrical with few short, thick and crooked pods. Seed of Florigiant are typical of Virginia type being large, elongated and round in cross section. Florigiant matures in approximately 135 days (Carver, 1969).

UF 78114 derived from a cross made in 1970 between Early Bunch and F 416-2 and is a composite of 9 lines. The pods and seeds of 78114 are larger than Florigiant. The growth habit is slightly more spreading than Early Bunch (Norden, 1983, personal communication).

UF 714021 is a line derived from the cross 427B and is closely related to the "Altika" variety released in Guyana. Plants have a bunch growth habit with the typical sequential branching pattern of Virginia botanical-type peanuts. The pods of UF 714021 are larger than those of Altika. UF 714021 matures in approximately 137 days (Norden et al., 1972).

The first set of crosses was made during the spring of 1981 in the greenhouse at the University of Florida Agronomy Farm and a further set of crosses was made during summer of 1982.

Four F_1 seeds from each 1981 and 1982 cross were increased in an off-season nursery in Puerto Rico during the 1981/82 and 1982/83 winter seasons, respectively.

Measurements on pod length, pod breadth, and pod constriction were taken on all 2-loculed pods from each F_1 plant of each cross. Figure 1 shows the profiles of the pod dimensions that were characterized.

Pod and seed trait data were not collected on single and 3-loculed pods. The use of 3-loculed pods in pod and seed trait characterization would tend to overestimate the true pod length and seed shape for a particular genotype. On the other hand, single loculed pods would underestimate pod length typical for the genotype, make it impossible to measure the diameter of pod constriction, and make it difficult to assess the true seed shape of a genotype.

Seed shape in this study is considered the presence or absence of the flat surface at the end where the two seeds meet inside a two loculed pod. Davidson et al. (1976) and Norden et al. (1982) identify flat seeds as those seeds that ride a round hole screen having a hole diameter 2.38 mm larger than the width of the slot in the slotted hole screen. Using this definition, it is possible to quantify the dimensions suitable for the identification of flat seeds. On the other hand, Coffelt and Hammons (1974a) identify flat seeds as those found within unconstricted pods. Seed in such pods have flattened ends where the two kernels meet. It is in this context that seed shape was scored in this study. Figure 2 shows seed of two of the peanut varieties used in this study, with contrasting seed shape characteristics (photo).

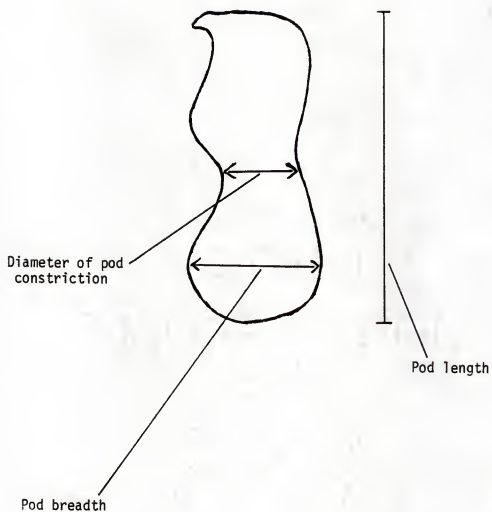


Figure 1. Profile of pod dimensions measured.



Figure 2. An example of contrasting seed shapes in two peanut genotypes used in the study.

Note: Chalimbana, on left, has unstricted pods and a flat seed shape.

Early Bunch, on right, has fairly well constricted pods and seeds are generally oblong with round, smooth surfaces.

After scoring for the F_1 pod and the F_2 seed traits, seeds from each 2-loculed pod were marked "A" or "B" depending on the position of the seed in the pod, i.e., apical seed were marked "A" and basal seed were marked "B". Each seed was then placed in a separate envelope for planting. A pedigree system of notation was used for identifying the individual seeds in the envelopes and the plants arising from them. This system enables the researcher to trace individual plants and lines back to their original parentage as well as to the specific position of the F_2 seed in the F_1 pods.

The F_2 seeds, as well as the parental seeds, were fungicide treated and planted in the field on June 2nd, 1982, at the University of Florida Agronomy Farm. The seeds were sown 60 cm apart within the row and 91 cm between rows. This spacing was chosen in order to minimize interplant competition. Cultural practices were performed following the guidelines used for commercial peanuts in Florida.

Naturally self pollinated F_2 fruits containing F_3 seeds were obtained at harvest, as well as fruits from parents. Fruits were obtained from the plants which had the identification tags attached following machine digging.

The time of harvest was based on accepted and previously described indicators of physiological maturity, such as; general yellowing of foliage, loss of lower older leaves, hardness and pronounced roughness of the external pod surface (Sturkie and Buchanan, 1973) and decrease in peg strength (Bailey and Bear, 1973).

Upon drying, well filled 2-loculed pods near the taproot were handpicked from each plant and bagged separately, each bag having been

labelled with the identification number of the plant. After the sample was dried further in the oven, a pod sample was withdrawn from each bag and F_2 pod and F_3 seed traits were scored for each individual pod in a similar manner as described for F_1 pods. The average pod length, pod breadth, and pod constriction was then calculated for that particular line.

Seed shape was not so easily quantifiable. The general tendency was that all the pods in a sample would yield the same seed shape for a particular F_3 genotype. However, in a few instances, it was apparent that the seed shape was variable even within the same pod sample. In this case, the recorded seed shape was the one in majority.

The remainder of the pods were then hand shelled and the seed was mixed with the seeds from the pod sample in preparation for planting replicated tests.

The April 1983 planting of field experiments consisted of the F_1 , F_2 , and F_3 for each cross together with the parents, arranged in randomized blocks replicated 3 times. Ten seeds were sown per row, 60 cm apart within the row and 91 cm between rows. Cultural practices were similar to those used for the F_2 plants the previous year.

Self pollinated F_1 , F_2 and F_3 fruits containing F_2 , F_3 and F_4 seeds, respectively, were obtained at harvest, together with fruits from the self pollinated parents. The same criteria used for harvesting and sampling F_2 plants in the 1982 season were used for harvesting and sampling the F_2 fruits in 1983.

A few representative plants per line were sampled in F_3 plants bearing F_4 seed, and pod samples from those plants were used for scoring for pod and seed traits as described earlier.

For the F_1 plants, only ten representative pods per plant were sampled from all F_1 plants for scoring pod and seed traits.

From all the pod measurements taken in all generations, one important variable could be obtained as follows: pod shape index = pod length/pod breadth. This variable, together with the pod constriction, was used to see if there was any correlation between the variable and the type of seed shape.

Methods of Analysis

Chi-Square Analysis of Segregation Data

The first F_2 data on seed shape were fitted to monogenic, digenic and trigenic ratios in order to explore which fitted the data best and provide the basis for genetic models and hypotheses on the inheritance of seed shape.

The F_3 and F_4 seed generation data were also used for testing the models and hypotheses, using chi-square techniques as described by Snedecor and Cochran (1967).

Heritabilities and Correlations

Estimates of heritability for the various traits and genotypic as well as phenotypic correlations among traits were obtained from variance and covariance component analysis using F_3 plant data. To facilitate the computations, seed shape data were coded 2 = flat-end shape and 1 = smooth-shaped seeds. The relevant parts of the analysis of variance and the mean square expectations are presented in Table 3.

Table 3. Relevant parts of the analysis of variance and mean square expectations for F_3 plants (F_4 seeds).

Source of Variance	df	Mean Square	Expectation of Mean Square
Total	5782		
Cross	9	M_4	$\delta^2_{pod} + k_1 \delta^2_{p(F,C)} + k_2 \delta^2_{F(c)} + k_3 \delta^2_c$
Family (Cross)	27	M_3	$\delta^2_{pod} + k_1 \delta^2_{p(F,C)} + k_2 \delta^2_{F(c)}$
Plant (Family Cross)	316	M_2	$\delta^2_{pod} + k_1 \delta^2_{p(F,C)}$
Pod (Plant Family Cross)	5430	M_1	δ^2_{pod}

The within family estimate of heritability was computed as follows:

$$h^2 = \frac{4/7 \delta^2_{p(F,C)}}{\delta^2_{p(F,C)} + \delta^2_{pod} \text{ (Plant, Family, Cross)}}$$

The genotypic correlation among the traits was computed as follows:

$$r_{g_{y_1 y_2}} = \frac{\text{Cov}_{p(F,C)} y_1 y_2}{\sqrt{\delta^2_{p(F,C)} y_1} \sqrt{\delta^2_{p(F,C)} y_2}}$$

The phenotypic correlation among traits was computed as follows:

$$r_{p_{y_1 y_2}} = \frac{\text{Cov}_{p(F,C)} y_1 y_2 + \text{Cov}_{pod(P,F,C)} y_1 y_2}{\sqrt{(\delta^2_{p(F,C)} y_1 + \delta^2_{pod(P,F,C)} y_1)} \sqrt{(\delta^2_{p(F,C)} y_2 + \delta^2_{pod(P,F,C)} y_2)}}$$

The relative efficiency of indirect selection for one trait (x) as a result of selecting for another trait (y) was calculated by the method of Falconer (1952) assuming the selection intensities for both traits

were equal and expressed as a percentage of response expected when selection was for the trait itself.

$$\frac{CR_x}{R_x} = \frac{h_y}{h_x} \cdot r_{g(x,y)} \times 100$$

where h_x , h_y and $r_{g(x,y)}$ were the square roots of the heritabilities and the genotypic correlation of (x) and (y), respectively. CR_x and R_x refer to the correlated response to indirect selection for trait (x) and to the direct response to selection for trait (x), respectively.

RESULTS AND DISCUSSION

Parental Generation

All parental lines bred true for presence or absence of flat seed shape as indicated by the observation on the seed shape type among plants of the parental rows interspaced among the offspring generations during the plantings of 1982 and 1983, with the exception of UF 714021.

Hybrid Generations

Assessment of the type of seed shape among the F_1 seed of each cross was not undertaken due to the fact that the pod, bearing the F_1 seed, is of maternal origin (Tan, 1972, and Godoy and Norden, 1981), and greatly influences the morphological traits of seed of the ensuing generation, such as seed shape and size.

However, measurements were first taken on F_2 seed contained in F_1 pods. Table 4 presents the means and ranges for pod length, pod breadth, pod constriction and type of seed shape. Also presented are the measurements undertaken on the parents of each cross.

Tables 5 and 6 present in a similar fashion the measurements taken on F_3 seed in F_2 pods and F_4 seed in F_3 pods, respectively.

The F_1 pod traits (i.e., pod length, pod breadth and pod constriction) from Cross 628 were generally intermediate between the parents involved (Table 4). Seed shape segregation showed more of the flat type of seed than the smooth type. There were no distinct differences in pod traits and seed shape among the progeny in both the original Cross 628 and its reciprocal.

Table 4. Means and ranges for Pod Length, Pod Breadth, Pod Constriction and seed shape for parents and F₁ pods bearing F₂ seeds.

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		mm		mm		mm		No.	
Chalimbana x UF 78114	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	628A1	42	(37 - 47)	16	(13 - 19)	14	(10 - 16)	22	9
	628A1i	45	(39 - 48)	17	(14 - 20)	15	(11 - 18)	22	10
	628A1ii	40	(36 - 43)	18	(15 - 18)	14	(10 - 17)	31	8
UF 78114	628A1iv	42	(37 - 48)	17	(14 - 19)	15	(12 - 18)	19	13
	UF 78114	44	(40 - 49)	15	(14 - 16)	13	(11 - 14)	0	10
UF 78114 x Chalimbana	UF 78114	44	(40 - 49)	15	(14 - 16)	13	(11 - 14)	0	10
	628B1	45	(38 - 49)	17	(14 - 21)	15	(13 - 18)	31	12
	628B1i	40	(36 - 43)	16	(13 - 20)	15	(11 - 20)	32	15
	628B1ii	42	(31 - 51)	16	(13 - 21)	15	(12 - 21)	22	5
Chalimbana x Early Bunch	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	629A1	37	(26 - 43)	15	(11 - 18)	12	(10 - 15)	31	21
	629A1i	41	(15 - 48)	16	(11 - 20)	14	(10 - 19)	52	12
Early Bunch	629A1ii	40	(31 - 44)	15	(13 - 18)	13	(11 - 17)	62	24
	629A1iv	39	(29 - 44)	17	(15 - 19)	15	(12 - 16)	63	10
	Early Bunch	42	(37 - 48)	15	(14 - 16)	12	(11 - 14)	1	9
Early Bunch x Chalimbana	Early Bunch	42	(37 - 48)	15	(14 - 16)	12	(11 - 14)	1	9
	629B1	42	(27 - 51)	17	(11 - 20)	14	(10 - 18)	49	10
	629B1i	42	(31 - 48)	17	(11 - 19)	14	(10 - 17)	43	9
	629B1ii	42	(27 - 49)	17	(12 - 19)	14	(9 - 17)	51	12
Chalimbana	629B1iv	43	(26 - 49)	17	(11 - 21)	14	(7 - 19)	34	19
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0

Table 4. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		mm		mm				No. ---	
Chalimbana x Florunner	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	630A1	34	(25 - 38)	15	(12 - 17)	13	(10 - 16)	41	0
	630A1i	33	(30 - 36)	16	(14 - 16)	13	(11 - 15)	34	5
	630A1ii	32	(18 - 35)	14	(14 - 15)	11	(9 - 12)	30	5
	630A1iv	37	(33 - 42)	14	(13 - 16)	12	(10 - 14)	23	7
	Florunner	29	(27 - 31)	13	(12 - 15)	11	(10 - 13)	10	0
Florunner x Chalimbana	Florunner	29	(27 - 31)	13	(12 - 15)	11	(10 - 13)	10	0
	630B1	33	(28 - 37)	15	(14 - 17)	12	(10 - 15)	45	8
	630B1i	36	(31 - 38)	17	(14 - 17)	14	(12 - 16)	58	7
	630B1ii	33	(29 - 36)	14	(12 - 16)	11	(10 - 14)	43	7
	630B1iv	29	(26 - 32)	13	(10 - 15)	10	(8 - 12)	67	15
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
Chalimbana x Florigiant	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	632A1	36	(32 - 40)	14	(12 - 17)	11	(6 - 14)	50	15
	632A1i	38	(30 - 43)	17	(12 - 19)	13	(10 - 17)	15	9
	632A1ii	43	(36 - 48)	18	(15 - 20)	15	(11 - 18)	18	8
	632A1iv	45	(40 - 48)	18	(16 - 20)	16	(12 - 19)	19	6
	Florigiant	41	(37 - 46)	17	(13 - 19)	15	(11 - 19)	0	10
Florigiant x Chalimbana	Florigiant	41	(37 - 46)	17	(13 - 19)	15	(11 - 19)	0	10
	632B1	42	(27 - 49)	18	(13 - 20)	12	(8 - 15)	29	7
	632B1i	44	(38 - 50)	19	(16 - 21)	14	(10 - 18)	23	14
	632B1ii	42	(35 - 48)	16	(13 - 19)	14	(11 - 18)	22	1
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0

Table 4. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		----- mm -----							
Chalimbana x UF 714021	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	634Ai	46	(40 - 52)	17	(15 - 18)	15	(10 - 17)	26	25
	634Aii	44	(38 - 49)	16	(16 - 19)	14	(10 - 18)	24	24
	634Aiii	43	(39 - 46)	17	(15 - 20)	15	(12 - 17)	28	4
	UF 714021	40	(37 - 45)	15	(13 - 17)	12	(9 - 14)	3	7
UF 714021 x Chalimbana	UF 714021	40	(37 - 45)	15	(13 - 17)	12	(9 - 14)	3	7
	634Bi	40	(34 - 47)	16	(14 - 19)	13	(8 - 16)	11	21
	634Bii	41	(38 - 44)	17	(16 - 19)	14	(11 - 16)	20	9
	634Biii	44	(39 - 47)	17	(16 - 19)	14	(9 - 16)	29	12
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0

a) i

ii A pedigree system of notation was used for identifying the original individual F₁
 iii seeds and the lines derived from them.
 iv

Table 5. Means and ranges for Pod Length, Pod Breadth, Pod Constriction and seed shape for parents and F₂ pods bearing F₃ seeds.

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		mm							
Chalimbana x UF 78114	Chalimbana	46 (37 - 56)	19 (17 - 20)	17 (15 - 21)	10	0			
	628A1	43 (36 - 46)	16 (14 - 18)	14 (13 - 16)	4	4			
	628A1i	44 (35 - 40)	17 (15 - 19)	15 (13 - 17)	9	2			
	628A1ii	41 (36 - 48)	16 (14 - 19)	14 (13 - 19)	3	8			
	628A1iv	42 (36 - 49)	17 (15 - 20)	15 (14 - 20)	4	6			
	UF 78114	43 (40 - 49)	16 (15 - 17)	14 (12 - 15)	0	10			
UF 78114 x Chalimbana	UF 78114	43 (40 - 49)	16 (15 - 17)	14 (12 - 15)	0	10			
	628B1	41 (35 - 49)	16 (14 - 18)	14 (11 - 17)	14	13			
	628B1i	39 (33 - 45)	16 (15 - 18)	14 (12 - 17)	95	71			
	628B1ii	43 (36 - 54)	16 (15 - 18)	14 (11 - 16)	86	21			
	Chalimbana	46 (37 - 56)	19 (17 - 20)	17 (15 - 21)	10	0			
Chalimbana x Early Bunch	Chalimbana	46 (37 - 56)	19 (17 - 20)	17 (15 - 21)	10	0			
	629A1	43 (37 - 51)	16 (13 - 18)	13 (10 - 16)	119	76			
	629A1i	43 (35 - 49)	16 (14 - 18)	14 (10 - 17)	115	60			
	629A1ii	41 (35 - 48)	16 (13 - 18)	14 (11 - 17)	123	58			
	629A1iv	39 (33 - 47)	16 (13 - 18)	14 (11 - 17)	238	130			
	Early Bunch	41 (35 - 49)	15 (14 - 17)	13 (11 - 15)	0	10			
Early Bunch x Chalimbana	Early Bunch	41 (35 - 49)	15 (14 - 17)	13 (11 - 15)	0	10			
	629B1	41 (34 - 51)	16 (14 - 19)	14 (11 - 17)	296	184			
	629B1i	42 (35 - 47)	16 (13 - 20)	14 (11 - 18)	157	93			
	629B1ii	41 (32 - 49)	15 (12 - 19)	13 (10 - 16)	175	108			
	629B1iv	42 (34 - 50)	16 (13 - 19)	13 (11 - 16)	74	23			
	Chalimbana	46 (37 - 56)	19 (17 - 20)	17 (15 - 21)	10	0			

Table 5. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		----- mm -----		-----		-----		----- No. -----	
Chalimbana x Florunner	Chalimbana	45	(39 - 55)	20	(17 - 23)	17	(16 - 20)	10	0
	630A <i>i</i>	31	(28 - 34)	14	(12 - 15)	11	(10 - 13)	21	3
	630A <i>ii</i>	30	(27 - 31)	13	(12 - 14)	11	(10 - 12)	140	7
	630A <i>iii</i>	32	(28 - 36)	14	(12 - 16)	12	(11 - 14)	24	3
	630A <i>iv</i>	33	(27 - 36)	13	(12 - 16)	11	(8 - 13)	20	2
	Florunner	29	(27 - 31)	13	(12 - 15)	11	(10 - 13)	10	0
Florunner x Chalimbana	Florunner	29	(27 - 31)	13	(12 - 15)	11	(10 - 13)	10	0
	630B <i>i</i>	33	(25 - 39)	14	(12 - 17)	12	(10 - 16)	192	17
	630B <i>ii</i>	32	(28 - 37)	14	(13 - 15)	13	(11 - 15)	53	9
	630B <i>iii</i>	32	(27 - 35)	14	(12 - 16)	12	(11 - 13)	310	31
	630B <i>iv</i>	32	(28 - 40)	14	(12 - 15)	13	(11 - 14)	50	8
	Chalimbana	45	(39 - 55)	20	(17 - 23)	17	(16 - 20)	10	0
Chalimbana x Florigiant	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0
	632A <i>i</i>	36	(29 - 42)	15	(11 - 17)	13	(9 - 15)	89	58
	632A <i>ii</i>	39	(31 - 44)	16	(12 - 18)	13	(9 - 16)	21	15
	632A <i>iii</i>	38	(31 - 44)	15	(13 - 18)	13	(9 - 17)	72	54
	632A <i>iv</i>	44	(40 - 48)	18	(16 - 19)	15	(12 - 19)	23	13
	Florigiant	41	(37 - 46)	17	(13 - 19)	15	(11 - 19)	0	10
Florigiant x Chalimbana	Florigiant	41	(37 - 46)	17	(13 - 19)	15	(11 - 19)	0	10
	632B <i>i</i>	37	(33 - 41)	15	(14 - 16)	12	(11 - 15)	48	26
	632B <i>ii</i>	41	(35 - 50)	17	(14 - 19)	14	(11 - 17)	42	22
	632B <i>iii</i>	42	(35 - 50)	18	(15 - 19)	15	(12 - 19)	50	32
	Chalimbana	45	(38 - 55)	19	(17 - 21)	17	(15 - 20)	10	0

Table 5. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		mm						No.	
Chalimbana	Chalimbana	46	(37 - 52)	19	(18 - 21)	18	(16 - 20)	10	0
	634Ai	41	(29 - 47)	16	(13 - 18)	14	(10 - 18)	219	20
	634Aii	38	(32 - 47)	16	(12 - 19)	13	(9 - 18)	77	13
	634Aiii	39	(32 - 46)	16	(12 - 19)	13	(10 - 17)	124	17
UF 714021	UF 714021	41	(38 - 45)	15	(13 - 17)	13	(10 - 15)	2	8
UF 714021	UF 714021	41	(38 - 45)	15	(13 - 17)	13	(10 - 15)	2	8
	634Bi	40	(33 - 47)	16	(14 - 17)	13	(10 - 15)	162	46
	634Bii	38	(33 - 43)	16	(13 - 18)	13	(11 - 16)	123	34
	634Biii	40	(34 - 51)	16	(14 - 19)	13	(11 - 16)	115	40
Chalimbana	Chalimbana	46	(37 - 52)	19	(18 - 21)	18	(16 - 20)	10	0

a) i

ii

iii

iv

A pedigree system of notation was used for identifying the original individual F_1 seeds and the lines derived from them.

Table 6. Means and ranges for Pod Length, Pod Breadth, Pod Constriction and seed shape for the parents and the F₃ pods bearing F₄ seed.

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		----- mm -----							
Chalimbana x UF 78114	Chalimbana	44 (35 - 53)	18 (16 - 24)	17 (15 - 19)	10	0			
	628Ai	43 (39 - 52)	18 (16 - 22)	17 (13 - 22)	12	5			
	628Aii	40 (39 - 48)	17 (14 - 19)	15 (13 - 17)	22	17			
	628Aiii	41 (38 - 45)	17 (15 - 19)	15 (14 - 18)	11	8			
	628Aiv	44 (37 - 48)	18 (15 - 19)	16 (14 - 19)	7	3			
	UF 78114	42 (40 - 47)	16 (15 - 17)	14 (12 - 15)	0	10			
UF 78114 x Chalimbana	UF 78114	42 (40 - 47)	16 (15 - 17)	14 (12 - 15)	0	10			
	628Bi	44 (36 - 52)	18 (15 - 23)	17 (14 - 20)	149	112			
	628Bii	42 (33 - 51)	18 (15 - 21)	16 (12 - 21)	101	65			
	628Biii	44 (32 - 60)	18 (15 - 21)	16 (14 - 21)	110	83			
	Chalimbana	44 (35 - 53)	18 (16 - 24)	17 (15 - 19)	10	0			
Chalimbana x Early Bunch	Chalimbana	45 (37 - 54)	19 (17 - 23)	17 (15 - 20)	10	0			
	629Ai	43 (33 - 51)	18 (14 - 21)	16 (13 - 20)	143	123			
	629Aii	43 (36 - 52)	18 (15 - 22)	17 (12 - 22)	181	160			
	629Aiii	42 (34 - 51)	18 (15 - 22)	17 (13 - 20)	214	177			
	629Aiv	43 (36 - 51)	18 (15 - 21)	16 (13 - 20)	172	145			
	Early Bunch	41 (36 - 49)	15 (13 - 18)	13 (12 - 15)	0	10			
Early Bunch x Chalimbana	Early Bunch	41 (36 - 49)	15 (13 - 18)	13 (12 - 15)	0	10			
	629Bi	42 (36 - 48)	18 (15 - 21)	17 (14 - 22)	230	171			
	629Bii	42 (35 - 53)	18 (15 - 21)	16 (13 - 20)	147	129			
	629Biii	42 (33 - 48)	18 (15 - 21)	16 (14 - 21)	175	152			
	629Biv	43 (37 - 49)	18 (16 - 19)	17 (15 - 18)	140	111			
	Chalimbana	45 (37 - 54)	19 (17 - 23)	17 (15 - 20)	10	0			

Table 6. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
Chalimbana x Florunner	Chalimbana	45	(39 - 52)	18	(16 - 19)	17	(15 - 19)	10	0
	630A1	31	(28 - 35)	15	(12 - 16)	13	(11 - 14)	12	3
	630A1i	32	(28 - 35)	14	(12 - 15)	12	(11 - 14)	9	0
	630A1ii	32	(29 - 34)	14	(13 - 15)	11	(9 - 14)	9	2
Florunner	630Aiv	34	(29 - 37)	16	(15 - 17)	14	(12 - 15)	5	0
	Florunner	30	(27 - 32)	14	(12 - 15)	12	(10 - 14)	10	0
Florunner x Chalimbana	Florunner	30	(27 - 32)	14	(12 - 15)	12	(10 - 14)	10	0
	630B1	35	(26 - 47)	16	(14 - 21)	15	(11 - 20)	202	0
	630B1i	34	(29 - 41)	16	(14 - 19)	16	(13 - 19)	194	5
	630B1ii	33	(27 - 41)	16	(13 - 18)	15	(12 - 18)	142	0
Chalimbana	630Biv	34	(29 - 41)	16	(14 - 19)	15	(13 - 18)	67	0
	Chalimbana	45	(39 - 52)	18	(16 - 19)	17	(15 - 19)	10	0
Chalimbana x Florigrant	Chalimbana	46	(39 - 53)	18	(17 - 19)	17	(15 - 19)	10	0
	632A1	37	(31 - 45)	17	(12 - 22)	15	(9 - 19)	126	106
	632A1i	40	(34 - 46)	17	(13 - 20)	15	(10 - 19)	157	139
	632A1ii	39	(31 - 44)	18	(13 - 20)	16	(10 - 20)	82	48
Florigrant	632Aiv	43	(40 - 49)	18	(16 - 19)	16	(13 - 19)	87	40
	Florigrant	42	(38 - 47)	17	(14 - 19)	15	(13 - 18)	0	10
Florigrant x Chalimbana	Florigrant	42	(38 - 47)	17	(14 - 19)	15	(13 - 18)	0	10
	632B1	38	(35 - 44)	17	(15 - 19)	15	(13 - 18)	55	43
	632B1i	41	(32 - 50)	18	(15 - 21)	17	(13 - 21)	122	83
	632Biv	40	(34 - 44)	18	(16 - 19)	17	(14 - 19)	71	51
Chalimbana	Chalimbana	46	(39 - 53)	18	(17 - 19)	17	(15 - 19)	10	0

Table 6. continued

Cross	Population and Cross Number ^a	Pod Length		Pod Breadth		Pod Constriction		Seed Shape	
		\bar{X}	Range	\bar{X}	Range	\bar{X}	Range	Flat	Smooth
		mm							
Chalimbana x UF 714021	Chalimbana	44	(37 - 51)	18	(16 - 20)	16	(15 - 20)	10	0
	634Ai	37	(29 - 47)	17	(14 - 20)	15	(12 - 19)	137	42
	634Ai1	38	(31 - 45)	17	(12 - 19)	15	(11 - 19)	94	22
	634Ai1f	40	(32 - 45)	17	(15 - 20)	16	(13 - 20)	119	42
	UF 714021	41	(37 - 46)	15	(12 - 17)	13	(10 - 15)	0	10
UF 714021 x Chalimbana	UF 714021	41	(37 - 46)	15	(12 - 17)	13	(10 - 15)	0	10
	634Bi	42	(30 - 50)	18	(15 - 22)	16	(13 - 22)	128	18
	634Bi1	40	(33 - 50)	17	(14 - 20)	16	(12 - 20)	37	24
	634Bi1f	41	(37 - 48)	18	(15 - 20)	16	(14 - 20)	59	8
	Chalimbana	44	(37 - 51)	18	(16 - 20)	16	(15 - 20)	10	0

a) i

ii A pedigree system of notation was used for identifying the original individual F₁

iii seeds and the lines derived from them.

iv

In Cross 629, there was a greater tendency for F_1 pod traits of the progeny to approach those of the smaller parent, Early Bunch, in both the original cross and its reciprocal. Segregation of seed shape showed more of the flat type of seed, associated with the touching of seed inside the pod, in both the original and its reciprocal cross.

In Cross 630, as in Cross 629, the F_1 pod traits showed a greater tendency to resemble the smaller parent, Florunner, than the Chalimbana pod traits. In addition, there was a marked shift towards the flat type of seed shape in both the original and its reciprocal cross. This was expected, since both parents exhibit a flat type of seed shape. It is possible that any smooth type of seeds in this particular cross arose mainly by sampling error.

An overview picture of Crosses 632 and 634 indicated that the F_1 pod traits were intermediately between the parents involved and segregation for seed shape was also mainly towards the flat rather than the smooth type of shape.

The F_2 pod traits of the progeny of Cross 628 resembled those of the smaller parent (UF 78114) more than those of Chalimbana, and there was no marked difference between the original and its reciprocal cross (Table 5). Seed shape segregation was towards the flat type of seeds more in the reciprocal than in the original cross.

In Cross 629, there was a greater tendency for F_2 pod traits to resemble those of the smaller parent, Early Bunch, in both the original cross and its reciprocal. A similar response pattern was observed among the progeny of this cross in the previous season. Segregation of seed shape was more towards the flat than the smooth type of seed shape.

In Cross 630, the response pattern was the same as in the previous season with the Florunner parent having a greater influence on F_2 pod traits than the Chalimbana parent. Seed shape segregation also showed a marked shift towards the flat type, since both parents have the flat type of seed shape.

In Cross 632, there is not clear cut picture observed, with F_2 pod traits of some progeny being intermediately between those of the parents and others being smaller than those of the smaller parent. This situation occurred both in the original and its reciprocal cross. As in the previous season, the flat type of seed showed up more frequently than the smooth type.

In Cross 634, the F_2 pod traits were generally intermediately between the two parents even though there was a tendency in some progeny lines to resemble the smaller parent (UF 714021) more than the Chalimbana parent. Seed shape segregated more for the flat than the smooth in both the original and the reciprocal cross.

The F_3 pod traits of Cross 628 were generally intermediately between the pod traits of the two parents in both the original and the reciprocal cross (Table 6). This is what was observed on pod traits among the F_1 progeny (Table 4) but not in the F_2 (Table 5). Seed shape segregation was similar to that observed previously among the progeny lines of this cross, with flat seed showing up more frequently than the smooth type.

In Cross 629, F_3 pod traits were also intermediately between those of the two parents, unlike the previous two seasons when pod traits resembled those of the smaller parent, Early Bunch, more than those

of Chalimbana. Seed shape segregated more for the flat than the smooth type and this was a consistent observation throughout the three seed generations.

In Cross 630 there is more evidence to show the greater influence of Florunner on pod traits among the progeny than that of Chalimbana. Throughout the three pod generations, the progeny pod traits resembled those of the smaller parent more than the Chalimbana parent, even though the pod size of the progeny was slightly enlarged as compared with the pod size of Florunner. Seed shape segregation clearly shows that any smooth types observed probably have arisen through sampling error.

in Cross 632, the F_3 pod lengths among the progeny were generally less than the pod lengths of the smaller parent, Florigiant, in both the original and the reciprocal cross. Seed shape segregated as in previous generations with more flat types than smooth types.

In Cross 634, most of the F_3 pod traits were intermediately between the two parents although there was a tendency for pod lengths to be shorter than those of the smaller parent. Seed shape segregation showed flat types more frequently than the smooth types as in previous seed generations.

The segregation of pod traits among the progeny of Cross 630, which involves Chalimbana and Florunner, is particularly interesting to note. In the F_1 , F_2 and F_3 pod generations, the pod traits of the progeny resembled the smaller parent more than the larger parent. Similar observations have been reported by other workers (Godoy and Norden, 1981; Chiow and Wynne, 1983) who noted that when the parents differed

substantially for the traits, as in the case of pod length, pod breadth and pod constriction, the smaller type was the dominant parent.

In addition, unlike Godoy and Norden, 1981, who observed only a few split pods in the progeny of the material in their study, an unexpectedly large number of split pods was observed among the progeny. This was apparently due to the growth of the larger seeds within the pods exerting pressure on the insufficiently strong shells. This observation would have important breeding implications in the improvement of the yielding capacity for Chalimbana if a small-podded line like Florunner is utilized as one of the parents.

Inheritance of Seed Shape

The F_2 seed segregation data in Crosses 628, 629, 630, 632 and 634 were tested for goodness-of-fit to a monogenic ratio of 3 flat-ended shape to 1 smooth-shaped by means of chi-square analysis. The data are presented in Table 7.

Chi-square values obtained for the Crosses 628, 629 and 632 and their reciprocal crosses were non-significant at the 5 percent probability level. Pooled chi-square values for the crosses and their reciprocals were also non-significant at the 5 percent probability level, indicating that the data fit the suggested monogenic ratio for the crosses involved.

The chi-square values for crosses 630 and 634 did not fit the proposed monogenic ratio of 3:1. This was expected for Cross 630, since both parents exhibit flat seed shape. Indeed, it was speculated that any observed smooth-shaped seeds in this population may have arisen due to misclassification of seed shape. As will be seen in

Table 7. F₂ seed segregation data in Crosses 628, 629, 360, 632 and 634 analyzed by chi-square test for goodness-of-fit to the ratio 3:1.

Parents	Cross Number	Number of F ₁ pods observed ^a		Total	χ^2	Probability of greater χ^2 value
		Flat Shape	Smooth Shape			
Chalimbana x UF 78114 UF 78114 x Chalimbana	628A	94	40	134	1.6816	0.10
	628B	85	32	117	0.3448	0.50
	Total	179	72	251	1.8180	0.10
Chalimbana x E. Bunch E. Bunch x Chalimbana	629A	208	67	275	0.0593	0.75
	629B	177	50	227	1.0705	0.25
	Total	385	117	502	0.7676	0.25
Chalimbana x Florunner Florunner x Chalimbana	630A	128	17	145	13.6299	<0.01
	630B	213	37	250	13.8720	<0.01
	Total	341	54	395	27.0388	<0.01
Chalimbana x Florigiant Florigiant x Chalimbana	632A	102	38	140	0.3428	0.50
	632B	74	22	96	0.2223	0.75
	Total	176	60	236	0.0225	0.75
Chalimbana x UF 714021 UF 714021 x Chalimbana	634A	78	53	131	16.6947	<0.01
	634B	60	42	102	14.2353	<0.01
	Total	138	95	233	30.9141	<0.01

^a F₁ pods bearing F₂ seeds.

Table 8. F₂ seed segregation data in Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.

Parents	Cross Number	Number of F ₁ pods observed ^a		Total	χ^2	Probability of greater χ^2 value
		Flat Shape	Smooth Shape			
Chalimbana x UF 714021	634A	78	53	131	0.5757	0.25
UF 714021 x Chalimbana	634B	60	42	102	0.2745	0.50
Total	Total	138	95	233	0.8393	0.25

in Tables 9, 10, 11, and 12, this speculation is given more weight considering the very low numbers of seed classified as smooth shaped.

The seed segregation data for cross 634 and its reciprocal significantly ($P < 0.01$) deviated from the expected ratio of 3:1, indicating that the mode of inheritance of seed shape in this population is distinct from that in other crosses. A different phenotypic ratio was tentatively applied (9 flat to 7 smooth) and the chi-square values did not significantly deviate from the expected ratio of 9:7, indicating that the data fits the suggested ratio. Table 8 shows the chi-square analysis test for goodness-of-fit to a 9:7 ratio.

Tables 9 and 11 show the chi-square analysis of seed segregation data in the F_3 and F_4 seed generations, respectively, of the crosses 628, 629, 360 and 632. The analysis of the F_3 and F_4 seed segregation data for cross 634 is provided separately in Tables 10 and 12.

The data in Table 9 was analyzed by chi-square test of goodness-of-fit to the ratio 5 flat:3 smooth (3AA:2Aa:3aa being the theoretical monogenic ratio in F_3 with self-fertilization) and the F_4 data in Table 11 was tested for goodness-of-fit to a 9:7 ratio for a similar reason.

The F_3 and F_4 seed segregation data for Crosses 628, 629 and 632 in both Tables 9 and 11, did not deviate significantly from the proposed ratios, thus giving further support to the proposed monogenic mode of seed shape inheritance in these Crosses.

As expected, however, seed segregation data for Cross 630 in both seed generations, deviated significantly ($P < 0.01$) from the expected ratio. There were far fewer pods containing smooth-shaped seeds,

Table 9. F₃ seed segregation data in Crosses 628, 629, 630, 632 analyzed by chi-square test for goodness-of-fit to the ratio 5:3.^a

Parents	Cross Number	Number of F ₂ pods observed ^b		Total	x ²	Probability of greater x ² value
		Flat Shape	Smooth Shape			
Chalimbana x UF 78114 UF 78114 x Chalimbana	628A	20	20	40	2.0000	0.10
	628B	195	105	300	0.8000	0.25
	Total	215	125	340	0.0294	0.75
Chalimbana x E. Bunch E. Bunch x Chalimbana	629A	595	324	919	1.9750	0.10
	629B	702	408	1110	0.2616	0.50
	Total	1297	732	2029	1.7533	0.10
Chalimbana x Florunner Florunner x Chalimbana	630A	205	15	220	88.3637	<0.01
	630B	605	70	675	211.9675	<0.01
	Total	810	85	895	299.4432	<0.01
Chalimbana x Florigiant Florigiant x Chalimbana	632A	205	140	345	1.3966	0.10
	632B	140	80	220	0.1213	0.50
	Total	345	220	565	0.4985	0.25

^a The theoretical monogenic ratio in F₃ with self-fertilization is 3AA:2Aa:3aa.

^b F₂ pods bearing F₃ seeds.

Table 10. F_3 seed segregation data for Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.

Parents	Cross Number	Number of F_2 pods observed		Total	χ^2	Probability of greater χ^2 value
		Flat Shape	Smooth Shape			
Chalimbana x UF 714021	634A	420	50	470	209.3291	<0.01
UF 714021 x Chalimbana	634B	400	120	520	90.3022	<0.01
	Total	820	170	990	284.1677	<0.01

Table 11. F_4 seed segregation data in Crosses 628, 629, 630, 632 analyzed by chi-square test for goodness-of-fit to the ratio 9:7^a.

Parents	Cross Number	Number of F_3 pods observed ^b		Total	χ^2	Probability of greater χ^2 value
		Flat Shape	Smooth Shape			
Chalimbana x UF 78114 UF 78114 x Chalimbana	628A	52	33	85	0.8382	0.25
	628B	360	260	620	0.8295	0.25
	Total	412	293	705	1.3918	0.10
Chalimbana x E. Bunch E. Bunch x Chalimbana	629A	710	605	1315	2.7234	0.05 ^c
	629B	692	563	1255	0.6288	0.25
	Total	1402	1168	2570	3.0091	0.05 ^c
Chalimbana x Florunner Florunner x Chalimbana	630A	35	5	40	15.8730	<0.01
	630B	605	5	610	456.8332	<0.01
	Total	640	10	650	470.6251	<0.01
Chalimbana x Florigiant Florigiant x Chalimbana	632A	452	333	785	0.5639	0.25
	632B	248	177	425	0.7637	0.25
	Total	700	510	1210	1.2606	0.25

^a The theoretical monogenic ratio in F_4 with self-fertilization is 7AA:2Aa:7aa.

^b F_3 pods bearing F_4 seeds.

^c Approaches the 5 percent value, 3.84, but is not quite significant.

Table 12. F₄ seed segregation data for Cross 634 analyzed by chi-square test for goodness-of-fit to the ratio 9:7.

Parents	Cross Number	Number of F ₃ pods observed ^a		Total	χ^2	Probability of greater χ^2 value
		Flat Shape	Smooth Shape			
Chalimbana x UF 714021	634A	350	106	456	77.9036	<0.01
UF 714021 x Chalimbana	634B	224	50	274	72.4090	<0.01
	Total	574	156	730	148.5397	<0.01

again giving support for the speculation that such smooth types of seed in this cross should have originated from possible misclassification of seed shape or by sampling error.

The F_3 and F_4 seed segregation data in Tables 9b and 10b for cross 634, deviated significantly ($P < 0.01$) from the proposed ratio and fail to support the segregation frequency observed for this population in the F_2 seed generation. The unusual segregation frequencies observed cannot be easily explained. They could be due to any of the following reasons: a) that the original parent (UF 714021) does not breed true to type as regards seed shape. Seed from the UF 714021 has been observed to have both the flat and smooth shapes in different pods obtained from the same parental plant (see Tables 4 and 5); b) could be due to possible misclassification of seed shape; or c) due to sampling error. Further studies are needed to determine which, if any, of these explanations is correct.

Proposed Genetic Model

The proposed gene symbols for five of the six parents used in these studies are given in Table 11.

Table 13. Proposed gene symbols for seed shape of the parents used in crosses to investigate the mode of inheritance of seed shape.

Parent	Phenotype	Genotype
Chalimbana	Flat end surface	SS
Florunner	Flat end surface	SS
UF 78114	Smooth, rounded end surface	ss
Early Bunch	Smooth, rounded end surface	ss
Florigiant	Smooth, rounded end surface	ss

The proposed genetic model assumes that seed shape in peanuts is inherited monogenically with the flat end shape (SS) being dominant over the smooth end surface (ss). Thus, when Chalimbana (SS) is crossed with UF 78114 (ss), for example, the F_1 pods from the cross should yield an F_2 seed shape segregation of 1SS:2Ss:1ss. However, since the flat end shape (SS) is dominant over the smooth end shape (ss), a phenotypic ratio of 3:1 is observed. The chi-square analysis test for goodness-of-fit has shown this to be true. In crosses involving Chalimbana (SS) and Florunner (SS), all seed in the progeny should be flat. The data here have yielded a few smooth types in such a cross, but this is most likely due to sampling error or possible misclassification of seed shape, or both. The proposed model seems to be strongly supported by data from the F_2 , F_3 and F_4 seed generations for Crosses 628, 629, 630 and 632.

This finding is in agreement with results reported by Hull (1937) and Balaiah et al. (1977), who found similar modes of seed shape inheritance in peanut, even though their seed shape classifications were different from the classification used in this study. Balaiah et al. (1977) concluded that kernel shape was inherited in a simple Mendelian ratio of 3 oblong:1 round whereas Hull (1937) obtained a clear cut ratio of 1 long:2 intermediate:1 short, with no detectable dominance.

This finding is, however, contrary to what Hayes (1933) reported. Hayes concluded that long seed was dominant over short seed in a ratio of 15:1, thus suggesting the presence of two factors governing the seed shape trait.

Such a discrepancy should be expected especially due to the tetraploid nature of the cultivated peanut where monogenic, digenic and trigenic ratios have been reported for the inheritance of some traits. It is possible that the parent UF 714021 used in this study could also be governed by a different set of factors in the control of seed shape. Further studies on this topic are needed.

Heritabilities and Correlations

Table 14 presents the heritabilities (h^2) of pod length, pod breadth, pod constriction index, pod shape index (i.e., pod length to pod breadth ratio) and seed shape together with the phenotypic (r_p) and genotypic (r_g) correlations among traits.

Estimates of heritabilities were generally low, ranging from 0.54 for pod length to 0.26 for seed shape. Low estimates of

Table 14. Phenotypic (r_p) and genotypic (r_g) correlation estimates among traits and their heritabilities (h^2).

	Pod Length	Pod Breadth	Pod Constriction Index ^a	Pod Shape Index	Seed Shape	h^2
Pod Length	r_p ---	0.79	-0.41	0.64	-0.51	54
	r_g --	0.82	-0.59	0.72	-0.41	
Pod Breadth	r_p --	--	-0.74	-0.40	-0.15	38
	r_g --	--	-0.89	0.53	0.43	
Pod Constriction Index	r_p --	--	--	-0.46	0.37	36
	r_g --	--	--	0.21	0.50	
Pod Shape Index	r_p --	--	--	--	-0.48	43
	r_g --	--	--	--	-0.62	
Seed Shape	r_p --	--	--	--	---	26
	r_g --	--	--	--	---	

^aPod constriction Index = 100/Pod constriction (mm).

heritability for pod length have been observed before (Badwal, 1965; Basu and Asoka Rajo, 1969; and Chiow and Wynne, 1983) generally in the range of the heritability estimate reported here. Other workers have reported high heritability estimates for pod length. Majumdar et al. (1969), Coffelt and Hammons (1974b), Mohammed et al. (1978) and Wynne and Rawlings (1978) reported high heritability estimates for pod length, ranging from 0.79 to 0.92.

Such discrepancies in estimates of heritability for a trait are to be expected since an estimate varies with the environmental conditions in which the plants were grown, the specific genetic population structure from which it was estimated (Cahaner and Hillel, 1980) and the method used to estimate the heritability (Coffelt and Hammons, 1974b).

Previous reports of heritability estimates for pod breadth have indicated high heritabilities (Majumdar et al. (1969) and Coffelt and Hammons, 1974b). A low estimate of heritability for pod breadth (0.38) was observed in this study, which can be explained using the same grounds as for pod length.

Since the heritability estimates for pod length and breadth were low in this study, then one would expect the heritability estimate for pod shape index (pod length/breadth ratio) to be low. As expected, the heritability estimate for pod shape index was low (0.43) and is contrary to the high estimate of heritability for pod shape index reported by Coffelt and Hammons, (1974b).

Heritability estimates have not been reported for pod constriction index and seed shape. In this study, low estimates of heritability for pod constriction index (0.36) and seed shape (0.26) were observed.

Genotypic correlations were generally higher than phenotypic correlations. Similar results in peanut have been found by other workers (Chioh and Wynne, (1983); Cahaner and Hillel (1980); Lin (1966); Layrisse et al. (1980) and Mohammed et al. (1978)).

Pod length was highly correlated both phenotypically and genotypically with pod breadth, suggesting that phenotypic selection for longer pods could result in broader pods. A similar conclusion is implied for pod breadth and pod constriction index which were negatively highly correlated both phenotypically and genotypically; i.e., selection for broader pods should result in pods with little or no pod constriction.

None of the four traits (pod length, pod breadth, pod constriction index and pod shape index) were positively highly correlated with seed shape.

Pod length had a relatively low negative correlations both phenotypically and genotypically with seed shape suggesting that selection for longer pods could result in pods with smooth seed shape. (It should be remembered that seed shape was coded as 2 = flat end shape and 1 = smooth shape to facilitate the analysis.)

Pod breadth had a low negative phenotypic correlation and a relatively low positive genotypic correlation with seed shape suggesting that phenotypic selection among the segregating population for pods with enlarged breadth may or may not result in pods with smooth seed shape depending on the genetic constitution of the population and the environmental conditions in which the population is grown. As such, pod breadth alone would seem to be an unreliable trait to select for if pods with smooth shaped seeds are desired.

The trait pod shape index had a low negative phenotypic correlation and a medium negative genotypic correlation with seed shape, suggesting that phenotypic selection for increased pod shape index could result in pods with smooth-shaped seed.

Pod constriction index had low positive phenotypic and genotypic correlations with seed shape. The values obtained in this study suggest (a) that phenotypic selection for pods with little or no constrictions could result in pods that have flat-end seed shape but (b) phenotypic selection of pods with constrictions could yield pods with the desirable smooth-shaped seeds.

Relative Efficiency of Indirect Selection of Trait (x) due
to Selection for Trait (y)

The results on genotypic and phenotypic correlations presented in Table 14 suggested that an analysis of the data be undertaken to determine the relative efficiency of indirect selection of trait (x) (i.e., improved seed shape) due to selection for trait (y) (i.e., pod length, pod breadth, pod constriction index, or pod shape index). Table 15 presents the relative efficiencies of selection expressed as percentages of the progress expected when selection was for the trait (x) itself.

The data strongly show that selection for improved (smooth) seed shape can best be achieved by selecting for smooth seed shape itself or by indirectly selecting for increased pod shape index. The pod shape index trait had a high negative association with seed shape (-101) suggesting that indirect selection for increased pod shape index would result in improved seed shape as efficiently as selecting directly for improved seed shape itself. This should be expected due

to the high (-0.62) genotypic correlation between pod shape index and seed shape, and also due to the relatively higher estimate of heritability for seed shape.

The next best alternative is to indirectly select for pod length which had a high (-92) negative association with seed shape in this study.

Table 15. Relative efficiency of indirect selection of trait (x) due to selection for trait (y).

Trait (y)	Relative efficiency of selection for trait (x) ^a			
	Pod Length	Pod Breadth	Pod Constriction Index ^b	Seed Shape
Pod length	---	108	-94	95
Pod Breadth		---	-97	68
Pod Constriction Index ^b			---	42
Pod Shape Index				---
Seed Shape				-101

^aRelative efficiency of selection expressed as percentage of the progress expected when selection was for trait (x) itself and (-) indicates negative association.

^bPod constriction Index = 100/Pod constriction (mm).

Breeding Implications

Improvement of seed shape is an important objective in many peanut breeding programs. This study should help improve the blanchability of the Chalimbana peanut through the genetic improvement of its seed shape.

Genetic analysis of the data has shown that seed shape has a low estimate of heritability (26 percent). The implication here is that in a breeding program, selection for improved seed shape would be more efficient in later generations (F_5 to F_6) rather than in earlier generations. Simmonds (1979) has emphasized that heritability is one component of response to selection and this means that traits with low estimates of heritability are better left till later generations before selection pressure for the desired trait is applied. This fact is empirically well known to plant breeders, so the heritabilities merely confirm the familiar.

The data on genotypic and phenotypic correlations together with the data on indirect selection have suggested that it is equally efficient to indirectly select for smooth-shaped seeds through selection of increased pod shape index. From experience obtained in this study, a pod shape index of 2.80 and above generally yields pods with smooth-shaped seeds. This value may vary with different peanut populations but would be a good indicator where improvement of seed shape is desired in the Chalimbana peanut variety.

SUMMARY AND CONCLUSIONS

A study was conducted to determine the mode of inheritance of seed shape in peanut (Arachis hypogaea L.). Estimates of heritability for pod length, pod breadth, pod constriction, pod shape index and seed shape were made. The genotypic and phenotypic correlations among the five traits were also determined. The study involved five crosses and their reciprocals and the progenies up to the F_4 seed generation were analyzed.

The following conclusions appeared to be justified from this study.

1. In four of the five crosses, the inheritance of seed shape is monogenically controlled with the flat-end shape (SS) being dominant over the smooth-end shape (ss). In one cross, the inheritance of seed shape was unknown probably due to the presence of other factors.
2. The estimates of heritability for the five traits were low, ranging from 0.54 for pod length to 0.26 for seed shape. This fact suggested that selection for improved (smooth) seed shape would be more effective in later generations rather than in earlier generations.
3. Genotypic correlations were generally higher than phenotypic correlations among traits.
4. The analysis of data to determine the relative efficiencies of indirect selection of related traits for the improvement of seed shape showed that seed shape improvement can best be achieved by directly selecting for seed shape itself or by indirectly selecting

for increased pod shape index. The next best alternative is through the indirect selection of longer pods.

LITERATURE CITED

- Badwal, S. S. 1965. Evaluation of genetic variability and correlation studies in a collection of groundnut varieties (Arachis hypogaea L.). Unpublished M. S. Thesis, Punjab Univ., Punjab, India.
- Bailey, W. K., and J. E. Bear. 1973. Components of earliness of maturity in peanuts, Arachis hypogaea L. Jour. Amer. Peanut Res. and Educ. Association. 5(1):32-39.
- Balaiah, C., P. S. Reddy, and M. V. Reddi. 1977. Genic analysis in groundnut: 1. Inheritance studies on 18 morphological characters in crosses with Gujarat narrow leaf mutant. Proceedings of the Indian Academy of Sciences. 85(5):340-350.
- Basu, A. K., and P. C. Asoka Rajo. 1969. Genotypic variability in some quantitative characters of groundnut. Sci. Cult. 35:408-409.
- Beasley, E. O., and J. W. Dickens. 1963. Engineering research in peanut curing. Technical Bulletin No. 155 North Carolina Agric. Expt. Station.
- Brown, P. 1965. A review of groundnut experiments in Malawi. Rhod. J. Agric. Res. 3:39-50.
- Cahaner, A., and J. Hillel. 1980. Estimating heritability and genetic correlation between traits from generations F_2 and F_3 of self fertilizing species: a comparison of three methods. Theor. Appl. Genet. 58:33-38.
- Carver, W. A. 1969. Registration of Florigiant peanuts. Crop Science. 9:849-850.
- Chow, H. V., and J. C. Wynne. 1983. Heritabilities and genetic correlations for yield and quality traits of advanced generations in a cross of peanut. Peanut Science. 10:13-17.
- Coffelt, T. A., and R. O. Hammons. 1974a. Inheritance of pod constriction in peanuts. The Journal of Heredity. 65:94-96.
- Coffelt, T. A., and R. O. Hammons. 1974b. Correlations and heritability studies of nine characters in parental and infraspecific cross populations of Arachis hypogaea. Oleagineux. 22(1):23-27.

- Davidson, J. I., V. Chew, and R. O. Hammons. 1976. An objective method for evaluating size and shape characteristics of peanut seed. Proc. Amer. Peanut Res. and Educ. Society. Vol. p. 27-43.
- Falconer, D. S. 1952. The problem of environment and selection. Amer. Naturalist. 86:293-298.
- Farouk, S. M., G. H. Brusewitz and M. R. Paulsen. 1977. Blanching of peanut kernels as affected by repeated rewetting-drying cycles. Peanut Science. 4(2):63-66.
- Gardner, E. J., and C. M. Woolf. 1950. The influence of high and low temperatures on the expression of tumorous head in Drosophila melanogaste. Genetics. 35:44-55.
- Gibbons, R. W., and J. R. Tattersfield. 1969. Out-crossing trials with groundnuts (Arachis hypogaea L.). Rhod. J. Agric. Res. 7:71-75.
- Godoy, I. J., and A. J. Norden. 1981. Shell and seed size relationships in peanuts. Peanut Science. 8:21-24.
- Hammons, R. O. 1973. Genetics of Arachis hypogaea. In: Peanuts-Culture and Uses. Amer. Peanut Res. and Educ. Assn., Inc., Stillwater, Okla. p. 135-173.
- Hassan, M. A. 1964. Genetic, floral, biological and maturity studies in groundnut. Unpublished M.S. Thesis. Ranchi Agric. Coll., Ranchi Univ., Kanke, Ranchi, India. 88 pages.
- Hayes, T. R. 1933. The classification of groundnut varieties. With a preliminary note on the inheritance of some characters. Trop. Agric. (West Indies) 10(2):318-327.
- Hull, F. H. 1937. Inheritance of rest periods of seeds and certain other characteristics in the peanut. Fla. Agric. Expt. Sta. Tech. Bul. 314.
- Hunter, H., and H. M. Leak. 1933. Recent advances in agricultural plant breeding. Blakiston, London. p. 340-341.
- Layrisse, A., J. C. Wynne, and T. G. Isleib. 1980. Combining ability for yield, protein and oil of peanut lines from South American centers of diversity. Euphytica. 29:561-570.
- Lin, H. 1966. Studies on the genetic behavior of quantitative characters in the hybrid progenies of virginia and spanish peanuts. J. Agric. Assn. China New Series 54:17-23.

- Mahmud, I., and H. H. Kramer. 1951. Segregation for yield, height and maturity following a soybean cross. Agron. Jour. 43:605-609.
- Majumdar, P. K., R. Prakash, and M. F. Hague. 1969. Genotypic and phenotypic variability in quantitative characters in groundnut. Ind. J. Gen. Plant Breed. 29(2):291-296.
- Mendel, G. 1865. Experiments in plant hybridization. In: Classic papers in genetics. James A. Peters (ed.). 3rd Ed. 1961. Prentice-Hall. 282 pp.
- Metelkcamp, H. R. R., and G. L. Hilderbrand. 1975. Changes in kernel quality of a long seasoned groundnut (Arachis hypogaea L.) variety during maturation. Rhod. J. Agric. Res. 13:21-22.
- Mohammed, J., J. C. Wynne, and J. O. Rawlings. 1978. Early generation variability and heritability estimates in crosses of virginia and spanish peanuts. Oleagineux. 33(2):81-86.
- Norden, A. J., H. A. D. Chesney, and A. P. Stephenson. 1972. Altika-A peanut variety for the tropics (Guyana). Fla. Agric. Expt. Sta. Circular S-215.
- Norden, A. J., J. I. Davidson, D. W. Gorbet and D. A. Knauff. 1982. Parent-progeny relationships for the flat seed trait in the Florunner cultivar. Proc. Amer. Peanut Res. Educ. Society. p. 40-49.
- Norden, A. J., R. O. Hammons, and D. W. Gorbet. 1977. Early Bunch-A new virginia-market type peanut variety. Fla. Agric. Expt. Sta. Circular S-253.
- Norden, A. J., R. W. Lipscomb, and W. A. Carver. 1969. Florunner-A new peanut variety. Fla. Agric. Expt. Sta. Circular S-196.
- Pchelarov, V. 1972. Deviations in phenotype from Mendelian segregations in pea. Referativny Zhurnal. (12) 55:1.
- Plunkett, C. R. 1926. The interaction of genetic and environmental factors in development. J. Exper. Zool. 46:180-244.
- Punnett, R. C. 1911. Mendelism. 34d Ed. The Macmillan Company, New York. 192 pp.
- Shackleford, P. S. 1972. Skin removal from spanish peanuts by heating to moderate temperature. Ph.D. Diss. Oklahoma State University, Stillwater, Okla.
- Simmonds, N. W. 1979. Principles of crop improvement. Longam Group Limited, London.

- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. 6th ed. Ames, Iowa State University Press.
- Sturkie, D. G., and G. A. Buchanan. 1973. Cultural practices. Chapter 9. p. 299-313. In: Peanut-Culture and Uses. Amer. Peanut Res. and Educ. Assn., Inc. Stillwater, Okla.
- Tan, N. V. 1972. The inheritance of pod pubescence in the peanut (Arachis hypogaea L.) and its relation to yield. Unpublished Ph.D. Diss. University of Florida, Gainesville, Fla.
- Tiemstra, P. J. 1973. Determining the quality of raw peanuts manufactured products. Chapter 12. In: Peanuts-Culture and Uses. Amer. Peanut Res. and Educ. Assn., Inc. Stillwater, Okla.
- Weber, C. R., and B. R. Moorthy. 1952. Heritable and non-heritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. Agron. Jour. 44:202-209.
- Woodward, J. D. 1973. The relationship of peanut milling quality to kernel tensile strength. J. Amer. Peanut Res. and Educ. Assn. 5:169-174.
- Wynne, J. C., and J. O. Rawlings. 1978. Genetic variability and heritability for an intercultivar cross of peanuts. Peanut Science. 5:23-26.

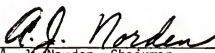
BIOGRAPHICAL SKETCH

Pickford K. Sibale was born in Dedza, Malawi, on November 21st, 1949. He graduated from Malosa Secondary School, Machinga, Malawi, in 1967. He received the Bachelor of Science degree in agriculture in July 1972, from the University of Malawi, and the Master of Science degree (plant breeding) from the University College of Wales, at Aberystwyth, United Kingdom, in June 1975. He completed the requirements for the Doctor of Philosophy degree in agronomy in April 1984, at the University of Florida.

He was employed as an Experimental Officer in the now defunct Agricultural Research Council of Malawi from August 1972 to August 1973 and from August 1975 to April 1976. From April 1976 to December 1980, he worked as a Research Officer for the Agricultural Research department in the Ministry of Agriculture and Natural Resources in Malawi.

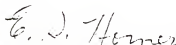
Pickford K. Sibale is married to the former Elizabeth Mary Minofu and is the father of a daughter and two sons.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



A. J. Norden, Chairman
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



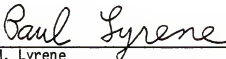
E. S. Horner
Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



D. W. Gorbet
Associate Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



P. M. Lyrene
Associate Professor of Agronomy

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



W. G. Blue

Professor of Soil Science

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

April 1984

Dean, College of Agriculture

Dean for Graduate Studies and Research